

EXPERIMENTAL STUDIES OF HEREDITARY INFLUENCES ON BEHAVIOUR*

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Introduction

IN 1883 Sir Francis Galton's concern with substituting a planned selection for natural selection in the interests of racial improvement resulted in his definite proposals for an applied science of "eugenics." The thinking and research which led to these proposals and to the later development of eugenics also created a "new" psychology, in which emphasis was upon the individual differences rather than the central tendencies in the behaviour of living organisms. Interest in *l'homme moyen* shifted to interest in the variations of behaviour in different strains, breeds and species. The research which followed this shift in interest demonstrated that the behaviour of living organisms — like their morphological, neurophysiological and biochemical characteristics — is influenced by hereditary factors. In no way did this deny that behaviour could be modified by environmental factors. Recent research has provided some grounds for the belief that the limits of the capacity for such modifications are themselves influenced by inherited properties of the organism. The intimate interactions of heredity and environment in the development of behaviour have become topics of the gravest importance to individuals and to social groups. It is with certain problems arising from the systematic study of such influences on behaviour that this paper is concerned.

The approach which is most likely to produce satisfactory answers to many of these problems is that of experimental genetics in which hereditary and environmental factors are controlled and systematically varied. Because of the techniques employed in this science man, with his cultural patterns of social behaviour and his long life span, is not

a suitable subject for research. The best one can expect to do is to study the behaviour of human subjects selected on the basis of certain hereditary and environmental relationships. As Professor Penrose has described it(30) :

"The data are provided by circumstances outside the control of the investigator and their study forms a descriptive and inductive science with some resemblance to astronomy as opposed to experimental physics."

A number of techniques have been developed which may be applied to these ends, the most popular in the past involving a comparison of the variation in behaviour of monozygotic twins with that of dizygotic twins. These techniques have been employed in an impressive number of studies, but the results have not been entirely unequivocal. Experimental "psychogenetics"† is limited by the fact that man cannot be employed as a subject for research, and human "psychogenetics" by serious limitations of the manner in which man, as a subject, can be manipulated. The advantages of supplementing one approach by the other should not be overlooked in the discussion to follow, which is concerned primarily with the experimental approach and, therefore, will not give human "psychogenetics" the attention it deserves in a complete picture of the genetics of behaviour.

The ultimate goals of the experimental approach are to determine whether or not specific behaviour patterns are influenced by genetic factors, and, if they are, to study the number and nature of the genetic factors involved, the location of the gene or genes on the chromosome, and the manner in

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† "Psychogenetics" is a term employed by Professor C. S. Hall in his excellent review of "The Genetics of Behavior" (21).

which the genes function in influencing the behaviour pattern. By examining typical attempts to reach these goals we shall see the research procedures which have been employed and gain some insight into the present state of knowledge concerning hereditary influences on behaviour. Of necessity the examples chosen for this purpose can represent only a small portion of the total available.

Behaviour Patterns Influenced by Genetic Factors

It is from the examination of differences in the behaviour of various strains, breeds, or species of animals that information concerning hereditary influences on behaviour is obtained. The student of "psychogenetics" can, and, in a number of cases, has taken advantage of the fact that different strains, breeds, and species of animals, some highly inbred, are already available for experimental observation. Such groups, differing initially in certain genetic characteristics other than the particular behaviour under study, are exposed to a set of stimulus conditions which elicit this behaviour. When consistent differences are observed between the responses of the various groups, conclusions concerning hereditary influences on the behaviour may be drawn. Similar comparisons may be made by selectively breeding animals of a heterogeneous parental population in which individuals differ in the particular pattern under study. A number of studies have employed the first of these general approaches, which I shall refer to as the comparison of strains. The particular behaviour patterns studied have been very diverse, but reference to a few may illustrate the type of information which may be provided by the application of this approach.

However, before we begin to examine this information it is important that a point be made regarding terms used to describe behaviour patterns studied in "psychogenetics." Terms such as "general activity," "savageness," "learning," and "emotionality," may appear to be vague and to lend themselves to many different interpretations. They need not be vague and difficult to

interpret if they are defined in terms of the actual operations employed in observing and measuring the behaviour they represent. An experimenter does not study "learning." He studies the behaviour of a particular organism in a particular type of maze under a particular set of circumstances. With practice the behaviour may show a progressive change of such a nature as to justify its inclusion in the class of phenomena called "learning." This class is a general one, containing many particular behaviour patterns, all of which have certain characteristics in common but which differ in other respects. Because it can be established that behaviour in a specific learning situation is influenced by genetic factors, it does not necessarily follow that "learning" as a class is likewise influenced. Indeed it has been shown that strains of animals bred for speed of learning under one set of maze conditions are not rapid learners in other maze situations(36), and animals bred for the excessive emotionality of their behaviour when exposed to certain forms of stimulation are not over-emotional when exposed to others.(4) In the following discussion it will be convenient to use short descriptive terms for a number of different behaviour patterns, but it should be kept in mind that these expressions are ultimately defined in terms of the actual operations employed in observing and measuring the behaviour they represent.

Anyone who has systematically observed the behaviour of infrahuman animals knows that striking inter-individual differences in levels of general or "spontaneous" activity occur even when such variables as age, sex and environmental conditions are controlled. It has been pointed out that such differences appear to be correlated with speed of learning, characteristics of responses during "experimental neurosis" and other complex forms of behaviour, and it has been suggested that these differences are "constitutional" in nature. This latter hypothesis, made on the basis of more or less casual observation, needs specific verification before it can be accepted as a valid statement of the facts. Some favourable evidence has come from comparisons of different breeds of

dogs.(1) The activity of animals representing a number of different breeds was measured in terms of the number of movements made during observational periods of twenty-four hours, the movements being recorded automatically. Analysis of the records revealed significant inter-breed differences of such a nature as to indicate the existence of three activity groups: breeds such as the German shepherd and cocker spaniel belonging to a "high" activity group; the British bulldog, dachshund and pekingese, to a "medium" activity group; and, the bassetthound to a "low" activity group. The records also showed that these differences were reflected primarily in the amount of nocturnal activity shown by the three groups: activity of the "active" group being distributed fairly uniformly during the twenty-four-hour test periods, the "medium" group being most active during the day, and the "low" group showing scarcely any movement at night. There is considerable evidence that this general or "spontaneous" activity is aroused by various types of internal stimuli, singly or in combination, and it is interesting that even such a non-specific form of behaviour appears to show the influence of genetic factors.

Comparisons of the "savageness" and "wildness" of various strains of animals have also revealed significant and consistent differences. Mallard ducks can be tamed in captivity while black ducks do not tame.(31) Wild rats and half-breeds from them, even though the latter were bred and reared in the laboratory, were significantly more "wild" and "savage" than quarter-breeds, yellow-hooded animals and pure albino rats.(37) These differences persisted throughout their lives, even though they had spent most of the time under the uniform environmental conditions of the laboratory, and the strains bred true. This "... strongly suggests that the differences arise from hereditary rather than environmental factors."

Other forms of behaviour are elicited by specific external stimulus conditions and follow a very stereotyped course. Some of these have been referred to as "tropisms." A very extensive series of experiments

(6, 7, 8) has indicated that one variety of tropism, geotropism, as it appears in young rats is significantly influenced by genetic factors. Young rats when placed on an inclined plane crawl up the plane; they are negatively geotropic. The angle at which an animal crawls up the plane is a function of the angle of inclination of the plane. The angles of orientation of three different strains of rats were measured, with the result that members of each inbred strain showed consistent functional relations between angle of orientation and angle of inclination of the plane, but different strains yielded characteristically different functions.

It should not be assumed because of the emphasis in this paper on genetic factors influencing behaviour that behaviour is not altered by an organism's life experiences. "Psychogenetics" is concerned with the nature of the genetic background upon which are projected modifications of behaviour during adjustment to environmental changes. Evidence is available which indicates that this capacity for modification—learning—is itself an inborn characteristic of living organisms. Some of this evidence comes from comparisons of different strains of animals. For example, one study(2) of albino, grey, agouti, chocolate and yellow mice showed consistent differences in learning performance among the different strains. Another study(3) compared the learning performance of normal control rats with that of a strain of inbred rats with less than normal brain weight. The latter learned more slowly than the former, and this difference consistently increased during the three generations studied.

There is evidence for genetic differences in the "emotionality" of animals. "Emotionality" was measured in terms of the number of defecations, urinations, attempts to escape, and position changes when the animals were placed individually for a standard period of time in strange and stressful environments. In one study(13) highly inbred grey Norway rats gave significantly higher scores than Wistar albino rats when members of each strain were exposed to the same test conditions. Another series of observations(40)

showed consistent differences between two strains of rats inbred for their maze-learning performances. The faster learners were more disturbed by non-maze situations than were the slow learners.

One of the most interesting stories in the present literature on experimental "psychogenetics" describes efforts to study the genetic basis of a certain type of "abnormal behaviour" usually referred to as "audiogenic seizures." Rats and mice have served as subjects for most of the experimental analysis, but the phenomenon has also been demonstrated in other animals. When the animal is confined and exposed to an auditory stimulus of relatively high frequency and intensity it may respond by a period of very violent running followed by apparent coma or by an epileptic-type convulsion. Not all animals respond in this manner, but several investigators have shown(12, 15, 20, 26, 27, 28) that certain strains have a significantly higher percentage of susceptible animals than do other strains. On the surface this would seem to support the view that genetic factors are operating. However, closer examination of the several experiments reveals a number of complications. One of these complications arises from apparently contradictory results obtained by two researchers(12, 16), one of whom found that wild grey Norway rats bred in captivity were highly susceptible to audiogenic seizures while the other obtained no seizures in a large group of trapped wild Norway and Alexandrine rats. Part of the difficulty here lies in the fact that little information was available as to how inbred the strains really were, but there are other difficulties, to which I shall refer later. More adequate control of the extent of inbreeding in the strains studied has been achieved in a series of observations on the susceptibility of mice to audiogenic seizures.(20) Two pure strains of mice were compared and one strain displayed significantly more hyperactivity, wall-jumping, wild circling activity, convulsions and dying, presumably from respiratory failure, than did the other.

A few studies have been concerned with the possibility that genetic factors may

influence the reactions of one animal to another of the same species—social behaviour. In one rather typical study(35) fighting between adult male animals was the form of social behaviour observed. The reactions of several strains of mice, all very nearly pure-bred, were compared under conditions which enabled the researcher to discard possible environmental factors as important variables. Indications of genetic differences were found between all except certain closely related strains, the basic behavioural characteristics of the strains showing "... wide differences, little variability, and no overlap under the conditions tested."

Such studies as these have capitalized on the fact that different strains, breeds and species of animals may differ in a number of characteristics, including their typical behaviour pattern. The general procedure has been to start with the different groups already established and to examine them for inter-group variations in behaviour. In a sense this procedure does not fulfill all the requirements of good experimental method. The independent variable, genetic constitution, has been varied by choice of subjects rather than by actual manipulation of subjects. However, the procedure has met other requirements of experimental method—systematic observation, control of variables such as external environmental conditions during observation, and measurement of specific behaviour patterns—and, therefore, greatly increases confidence in the interpretation of results. The casual observer of animal behaviour may ask what is new about the information obtained by application of the procedure just discussed. He may say that he has often "seen" differences in the behaviour of different strains, breeds, or species. By applying the procedures of experimental "psychogenetics" it becomes possible to go far beyond the general impressions of the casual observer by stating how significant the observed differences are, that they do in fact represent the influences of genetic rather than extragenetic factors, and, eventually, by learning a great deal more about the nature of the genetic factors

involved than casual observation could ever divulge.

The second general procedure employed in determining whether or not a particular behaviour pattern is influenced by genetic factors reverses the order of events characterizing the procedure we have just discussed. It involves first measuring the behaviour pattern as it appears in a heterogeneous parental generation and then inbreeding under uniform-environmental conditions those animals exhibiting the pattern and those not exhibiting it. When the behaviour can be measured along a continuum inbreeding may be carried on in family lines from parents exhibiting the behaviour to different degrees. If the behaviour is influenced by heredity such selective breeding after a number of generations results in strains that breed more or less true for the behaviour under examination. In order to produce pure strains, the inbreeding frequently has been limited to the particular family lines initially selected from the parental generation.

A study of two strains of rats selectively bred, one for activity and the other for inactivity, clearly illustrates the use of this method and the necessity for precautions in limiting inbreeding to selected family lines.(33) Activity was measured in terms of the number of revolutions turned by the animals in a revolving drum during a standard test period before feeding time. Precautions were taken to feed the animals at the same hour each day, to keep them in darkness during the test period, and to control extraneous stimuli in the observation room. Inbreeding was carried out at both extremes of the distribution of activity. During the first four generations care was not taken to breed within family lines, and the results clearly show the effects, for not until the fifth generation when ancestry did become a consideration in the breeding was the difference between active and inactive strains significant. With continued inbreeding of family lines two strains were finally established which showed consistent differences in activity level—one being highly active ; the other, highly inactive.

Some of the most extensive selective breeding experiments have involved the maze-learning behaviour of rats. One of these studies(39, 40) used a 17-unit multiple-T maze as the problem to be learned. Throughout the eighteen filial generations during which selective mating was continued, each animal, at the time of test for speed of learning, was given nineteen trials in the maze, the total number of errors occurring during these trials serving as the measure of behaviour. The parental generation consisted of an unselected, heterogeneous sample of rats. Selective breeding was accomplished by "... mating together the brightest rats within each of the brightest litters, the dullest within each of the dullest." The separation of two strains—"maze bright" and "maze dull"—was definitely noticeable by the second filial generation and, by the seventh generation, there was practically no overlapping between them. Other studies, similarly conducted, have yielded comparable results.

Another example of selective breeding for a specific behaviour pattern appears to have verified the conclusion arrived at by comparison of strains that susceptibility to audiogenic seizures in rats is affected by genetic factors.(15) The parental generation was divided into two groups, one of which consisted of animals having seizures in 50 per cent or more of the standardized test trials and a second with seizures in less than 50 per cent of the trials. Matings between highly susceptible animals and between animals of low susceptibility as well as between animals from both of these groups were carried on for six generations. By this time evidence of consistent trends toward increases in high and low susceptibility to seizures had become apparent, suggesting that genetic influences were involved.

A selective breeding experiment(18, 19) of particular importance to those interested in the study of behaviour disorders was designed to investigate the "emotional" behaviour of rats exposed to a mildly stressful situation, in which quantitative measures of "emotionality" could be obtained. The reactions of a heterogeneous parental genera-

tion were measured and inbreeding carried on for twelve filial generations by mating together "emotional" animals to produce an "emotional" strain and "non-emotional" animals to produce a "non-emotional" strain. The magnitude of the difference between these two strains increased until the ninth generation, when it became relatively stable.

Perhaps you have noted that, in illustrating the ways in which these two general approaches have been applied, I have selected several behaviour patterns the genetic bases of which have been examined by both. In the vast majority of cases information obtained by one approach has confirmed that obtained by the other. The diversity of behaviour patterns studied and theoretical considerations regarding the nature of the behaviour lead us to believe that hereditary factors influence all behaviour to some degree. We have seen that such influences are operating in general activity and specific tropistic responses, in adjustment to external environment conditions through learning, in "emotional" reactions to environmental stresses, in the "abnormal" behaviour of audiogenic seizures and even in certain social acts involving two or more members of the same species. The application of experimental methods has added objective support to our beliefs concerning the roles of genetic factors in behaviour and has provided means of obtaining more precise information as to the way in which these roles are played.

The Nature of Genetic Factors Involved

When it is established that a specific behaviour pattern is influenced by heredity the question arises as to the number and nature of the genetic factors involved. The experimental methods which geneticists have developed to answer this question require the use of two or more pure strains differing in the behaviour under study. By crossing two inbred strains and later their first generation hybrids, by backcrossing these hybrids to either parental strain or by outcrossing them to any other strain, variations in the behaviour of offspring may result which justify

conclusions concerning the number of genetic factors involved in the behaviour and the nature, for instance dominant or recessive, of these genetic factors. To date relatively few studies have reached this point in the genetic analysis of behaviour and, of those that have, only a few have presented unequivocal results.

As you may recall, studies of geotropic responses of young rats showed that different strains of animals breed true for certain geotropic constants but that these constants differ in magnitude from strain to strain. Crosses between two such strains have produced hybrids which, according to the researchers(9, 10) are identical in their geotropic responses with the parents of one strain. These results have been interpreted as indicating that rather simple dominance relations exist between homologous genetic factors from the two strains.

It would not seem right to discuss "psychogenetics" without some reference to "waltzing" mice, for they provide some interesting examples of the application of Mendelian principles. In one very early investigation(11) a pure line of Japanese waltzing mice was mated with a pure line of European albino mice. The first filial generation contained no waltzers and breeding within this generation produced offspring in the ratio of four normal to one waltzer (close to the 3:1 proportion expected with recessive inheritance). This picture of genetic factors operating to influence behaviour, when supported by subsequent studies, suggested that waltzing was transmitted as a recessive unit character.

Other neuromuscular abnormalities, characterized by trembling of the limbs and body and accompanied by deficient growth, and death before five weeks of age, have been observed in certain strains of deer mice.(24) Since all affected individuals were produced by related unaffected parents it appeared that this syndrome was "due to a recessive mutation of a single gene locus. . ."

One investigator(23) has described a strain of what he called "clumsy" pigeons or "homeless homers." The behaviour of these birds resembled that of a blind pigeon,

although it was established that they could see. According to the investigator, "They grope their way about, walk off precipices, crash into walls during flight, fumble their food, and would be quite incapable of surviving in the wild state." This behaviour appeared initially in the offspring of normal pigeons, which suggested that its genetic constitution was simple and recessive in nature. This hypothesis was supported by further breeding in which crosses between "clumsy" animals produced only "clumsy" offspring, while outcrosses yielded only normal offspring.

These are examples in which the number and nature of the genetic factors influencing behaviour patterns appear to be relatively simple. But as we would anticipate, this is not always the case. Let us return for the moment to the mystery of the audiogenic seizure. Genetic analyses of this behaviour pattern as it appears in rats have led researchers to propose three different types of genetic constitution, a result which appears to be a function of the fact that impure strains of animals were used. The observations of two investigators(27) indicated that the seizure frequency of susceptible offspring of two susceptible parents was only slightly greater than that of susceptible offspring of one non-susceptible and one susceptible parent. From these results they concluded that "susceptibility is transmitted as a unitary character," and that "it is transmitted as a dominant trait." On the basis of a later study(26) one of these researchers altered his opinion and "concluded that the hereditary nature of the transmission of convulsive tendencies is complex in nature." Observations by a third investigator led him to postulate that two pairs of genetic factors influence susceptibility to audiogenic seizures. It appears from all this that genetic factors are at work in the manifestations of this behaviour pattern in rats, but, as regards the number and nature of the factors involved, "you pay your money and you take your choice." The best designed genetic analysis of audiogenic seizures so far available(43) employed as subjects two pure strains of house mice which differed greatly in the

number and severity of seizures. All necessary crosses were carried out and, with one exception, the results conform to what would be expected were audiogenic seizures "inherited as a single dominant gene." But the story is still not complete, for another investigator, using another genus of mouse, has obtained results which strongly suggest that susceptibility to audiogenic seizures is inherited as a single recessive gene.(21) Since these two experiments on mice appear to have been adequately designed and conducted, the differing results may mean that the genetic constitution of the same behaviour pattern in different genera may be different, a point of considerable potential importance in "psychogenetics."

The importance of starting a genetic analysis of behaviour with pure strains of animals becomes particularly apparent when the literature is searched for examples in which several sets of factors—multiple factors—act together in affecting the same behaviour pattern. If pure lines are crossed and multiple factors are involved the first filial generation should show uniform behaviour and the second generation, a wide variability in behaviour.(34) Several investigators have advanced hypotheses that behaviour patterns such as general activity(5), maze learning(39) and "emotionality"(21) are affected by multiple genetic factors, but they have obtained inconclusive results when the hypotheses were tested, primarily because impure strains of animals were used.

Other complications which may arise during attempts to determine the nature of genetic factors affecting behaviour are illustrated by two breeding experiments(41, 42) involving selection in dogs of "aptitudes" useful in hunting and other kinds of work. The behaviour patterns studied were those least affected by training and which appeared very early in the life of the dog. In one case dogs of a breed which gives tongue on the trail while pursuing game were mated with dogs of a breed which trails mutely. All the offspring gave tongue on the trail but had the type of voice characteristic of the parents who trailed mutely. In the other

study bodily appearance and certain behaviour patterns characteristic of hunting were examined. The first crossing of pure breeds revealed the operation of dominance or partial dominance, but further generations did not indicate any clear or simple Mendelian segregation of the behaviour patterns involved. Second generation crosses produced offspring who, in some cases, resembled one pure breed in appearance but showed the behaviour patterns of the other parental breed.

From what has been said it is obvious that those interested in the genetic analysis of behaviour patterns have set about their task by utilizing research designs already available in biogenetics. Presumably they will continue this practice when they have developed their field of study to the point where they can attack the problems of mapping chromosomes and of determining the precise way in which genes influence particular behaviour patterns. As yet but little information is available which even begins to touch on these problems.

The exchange of homologous parts between chromosome pairs during the development of germ cells provides a means for locating genes on chromosomes. This process of "crossing over" is evidenced by the separation of "linked" characteristics which have consistently appeared together in past generations. "With the exception of some of the neuromuscular disorders, e.g. waltzing, shaker, and pirouetting, there is no information regarding the location of the genes on the chromosomes for behaviour characters." (21) Recent research (25) has shown that there are in a number of animal species many cases where behaviour patterns are associated with coat colour genes, and it has been suggested that "the associated coat colour genes may be used as genetic markers of such traits. When so employed, it will be possible by manipulating the coat colour markers to synthesize new combinational trends in morphology physiology, and resultant behaviour for psychological study."

Any scientific approach to the study of behaviour must recognize that all behaviour patterns are dependent upon and limited by

the morphological, neurophysiological and biochemical characteristics of the organism. It is through such characteristics that genetic factors exert their influences on behaviour. As yet there is very little information available as to how such genetic factors function in producing their effects. In one study (3) referred to earlier, significant differences were found between the speed of learning of normal control rats and of a strain of inbred rats with less than normal brain weight. Although it is not altogether surprising that variations in the characteristics of the brain are associated with variations in complex behaviour patterns, the study does illustrate one approach to the problem of how genetic factors may produce their effects on behaviour. Another approach has involved comparisons of various structures in animals from strains differing in certain behaviour patterns. Attention has been focused on such structures as the endocrine glands in emotional and non-emotional strains of rats and brain weights of "maze bright" and "maze-dull" animals. Comparisons of physiological processes in different strains also have been made, respiratory metabolism of active and inactive strains of rats being an example. In other experiments (38) extensive environmental variations have been introduced during tests of different strains for the behaviour characteristics in which they differed. If such environmental variations had the effect of upsetting the differences between strains some clue might be obtained as to the mechanism by which the genetic factors involved were influencing behaviour.

Interaction of Heredity and Environment

Early studies of eugenics have pointed to the fact that individuals showing certain types of behaviour patterns, i.e. low general intelligence and neuro-psychiatric breakdown, often had family histories of similar behaviour patterns in previous generations. The tendency was to interpret such information as indicating an hereditary basis for the behaviour in question. Studies of the interactions of heredity and environment in the development of behaviour soon showed the potential fallacy of such conclusions, for this

type of information is not adequate to rule out the possibility that the family environment is a major contributing cause.

In discussing methods for studying the influences of genetic factors on behaviour the necessity for controlling the environment in which the organism develops has been emphasized. But this is not always as simple as it may appear on the surface to be.(34) In some instances important environmental factors may not be recognized and, hence, go uncontrolled. In other instances adequate controls may be difficult to achieve.

Earlier in this paper it was remarked that one of the most interesting series of studies in "psychogenetics" has been that in which possible genetic influences on audiogenic seizures have been examined. From what has been said so far it appears that the susceptibility of rats to such seizures does have a genetic basis and that multiple genetic factors are probably involved. But there are two important considerations of an environmental nature which complicate any such conclusions. Research(14) has shown that, not only does susceptibility change with age, but that the nature of the sound stimulus used to induce the seizures has an effect on the age of maximal susceptibility. If this is true, as it seems to be, it is possible that the number of animals in any particular generation of any particular strain which show the behaviour may vary as a function of the organismic variable of age and/or the environmental variable of the nature of the auditory stimulus. Apparently contradictory conclusions might be drawn from different genetic studies in which these two variables were not subjected to identical controls. It has also been shown(29) that in one colony of rats the vast majority of those susceptible to audiogenic seizures were suffering from purulent otitis media, while those not susceptible very seldom showed this form of middle-ear infection. I have been informed by members of another laboratory that this relation between susceptibility and infection approaches a perfect correlation when more refined methods of examining for infection than those used in the initial study are employed. It is possible, if this

relation is a valid one, to account for results obtained in certain genetic studies of susceptibility to audiogenic seizures in terms of differential exposure to infection. Matings between two susceptible animals might be expected to provide greater exposure of offspring to infection than matings between non-susceptible animals and matings of susceptible with non-susceptible animals might be expected to occupy an intermediate position between these extremes. In the earliest genetic study of audiogenic seizures(27) the rank order of percentages of susceptible offspring resulting from these three types of matings is exactly as would be predicted from these assumptions. This does not establish the validity of the assumptions but it does illustrate a type of complication that may cause serious misinterpretations of experimental results in which differences between strains have been found.

Recent research has indicated how very rapidly behaviour patterns may be learned in the period immediately following birth. One writer on the subject(22) has suggested: "Much that we attribute to instinct, because no *prolonged* learning is evident, might thus be due to learning that needs only a few seconds for completion." In many species one of the most important environmental influences during early development is the interaction between parents and offspring. It is very probable that much of the early behaviour of the offspring is affected by learning resulting from this interaction. If parents have behaviour patterns differing significantly from those of other parents it is perfectly possible that the young of these parents may also differ in their behaviour, not because of genetic differences but because they have been exposed to different learning situations. Let me give a hypothetical example to make this point more specific. If we are interested in searching for possible genetic factors influencing susceptibility to breakdown under stress referred to as "experimental neurosis" in the early research literature, we might decide to breed selectively animals breaking down easily and those very resistant to breakdown. The offspring of these two lines would at some

stage in their development be tested for susceptibility. The results of several generations of such inbreeding might, and I predict would, be two strains of animals, one very susceptible to stress and the other very resistant. We might then be inclined to say that susceptibility to breakdown under stress is influenced by genetic factors. In so doing we would be overlooking a potentially important environmental variable had we not taken the precaution to examine the effects which rearing by a susceptible mother as compared with rearing by a resistant mother might have on the behaviour of the various offspring during the tests for susceptibility. Significant differences in the behaviour of offspring from the two lines might be accounted for partially or wholly in terms of environmental differences resulting from interaction with the two types of mother rather than in terms of genetic differences. On the basis of his own observations one writer(32) has suggested that environmental factors of this order are operative in the appearance of "wildness" in rats, which depends to some extent upon whether or not the offspring are reared by a wild mother and whether or not they are reared with other wild rats.

These interactions of genetic and environmental factors may be summarized in terms of an analysis of the general courses of phenotypic variation.(34) There appear to be three main paths by which genetic and environmental factors can influence a specific behaviour pattern. The first is that deriving from the genetic characteristics of the organism showing the behaviour. A behaviour pattern, at least in certain species, can also be affected by the maternal environment, which in itself is determined partly by the genetic constitution of the mother and partly by the mother's previous reactions to her physical environment. This constitutes a second path. The remaining path consists of environmental influences which are entirely independent of the genetic constitution of the stock to which the individual belongs. It is because all these paths may be involved to some extent in the manifestation of any behaviour pattern that the interaction of

heredity and environment is a major concern in experimental "psychogenetics." As Professor Haldane has written(17): "The interaction of nature and nurture is one of the central problems of genetics. We can only determine the differences between the different genotypes by putting each of them into a number of different environments. We compare two pure lines of mice not only as regards colour, hair form, and other characteristics which are little affected by nurture, but for such characters as resistance to different bacterial and virus infections, each of which must be tested by appropriate changes of environment."

There are other reasons for being interested in the interactions of heredity and environment. Investigators responsible for most of the studies already discussed were motivated by a desire to understand the basic principles underlying genetic influences on behaviour, but there are those whose main concern is with the practical problems of developing strains with characteristics of adjusting to particular environments. Breeding in this latter case is for genotypes that are suitable for particular types of environment and not for a "super"-genotype most effective in all environments. The wide diversity of physical and social environments in which infrahuman animals and man must live and work may not be at all consistent with concepts of a super-race or a super-man. From the research point of view this suggests the practical value of studying the interactions of heredity and environment in influencing the behaviour of different strains, breeds, and species of animals under a variety of different environmental conditions.

Conclusion

If time and your indulgence permitted, this discussion could be made much more complete, but I doubt that increasing the number of examples of behaviour influenced by genetic factors would alter very much the general impression which this brief examination of contemporary experimental "psychogenetics" conveys. Certainly knowledge in this area is fragmentary and in need of much

supplementation. There is no doubt in my mind that the importance of this field of experimentation warrants the effort necessary to develop it as a systematic and reliable discipline. There are many important principles of behaviour which can *only* be discovered and clarified by research of this kind. During several years of investigation into problems of experimental psychopathology I have been particularly impressed with the importance of this point of view. There is a wealth of circumstantial evidence suggesting that the development of "abnormal" behaviour patterns under the stresses of environmental circumstances is to some extent influenced by genetic factors. Since behaviour disorders analogous to those in man can be produced in infrahuman animals under controlled conditions there seems to be no reason why application of the methods of experimental "psychogenetics" cannot help greatly in clarifying and extending our knowledge of psychopathology. Selective breeding of infrahuman animals for susceptibility to breakdown under stress might well result in the development of susceptible and resistant strains. Once such strains were available it would be possible to proceed to the genetic analysis of the behaviour, to examine the relations between it and other psychological characteristics of the animals, and to determine the effects of varying the environmental stress conditions on the differences of behaviour between the two strains. Since these differences in reactions to stress are undoubtedly reflected in morphological, neurophysiological, and biochemical differences between the strains, it also would be possible to compare various organs and processes within the animals, thus obtaining valuable information concerning the physical correlates of behaviour disorders. Such an approach to these very important problems of adjustment could not employ man as its subject. It is illustrative of the valuable roles which the methods of experimental "psychogenetics" can play in understanding the influences of heredity on behaviour.

By now you may have suspected that I am somewhat enthusiastic about the promise experimental "psychogenetics" gives for

future contributions of importance to the understanding of the behaviour of man and his infrahuman relatives. If I have not conveyed this enthusiasm to you the failure is on my part and cannot be attributed to any lack of inherent interest or importance in the experimental study of hereditary influences on behaviour.

REFERENCES

1. Anderson, O. D. (1939). "The spontaneous neuromuscular activity of various pure breeds of dog and of inter-breed hybrids of the first and second generation." *Amer. J. Physiol.*, **126**, 422-3.
2. Bagg, H. (1920). "Individual differences and family resemblances in animal behavior." *Arch. Psychol.*, **6**, 1-58.
3. Bassett, G. C. (1914). "Habit formation in a strain of albino rats of less than normal brain weight." *Behav. Monogr.*, **2**, 1-46.
4. Billingslea, F. Y. (1941). "The relationship between emotionality and various other salients of behavior in the rat." *J. comp. Psychol.*, **31**, 69-77.
5. Brody, E. G. (1942). "Genetic basis of spontaneous activity in the albino rat." *Comp. Psychol. Monogr.*, **17**, No. 5.
6. Crozier, W. J., and Pincus, G. (1929). "Analysis of the geotropic orientation of young rats." I and II. *J. gen. Physiol.*, **13**, 57-119.
7. Crozier, W. J., and Pincus, G. (1931). "Analysis of the geotropic orientation of young rats." III. Parts 1 and 2. *J. gen. Physiol.*, **15**, 201-42.
8. Crozier, W. J., and Pincus, G. (1931). "Analysis of the geotropic orientation of young rats." IV. *J. gen. Physiol.*, **15**, 243-56.
9. Crozier, W. J., and Pincus, G. (1935). "Analysis of the geotropic orientation of young rats." IX. *J. gen. Physiol.*, **19**, 211-20.
10. Crozier, W. J., and Pincus, G. (1936). "Analysis of the geotropic orientation of young rats." X. *J. gen. Physiol.*, **20**, 111-44.
11. Derbyshire, A. D. (1902). "Note on the results of crossing Japanese waltzing mice with European albino races." *Biometrika*, **2**, 101-4, 165-74, 282-5.
12. Farris, E. J., and Yeakel, E. H. (1943). "The susceptibility of albino and grey Norway rats to audiogenic seizures." *J. comp. Psychol.*, **35**, 73-80.
13. Farris, E. J., and Yeakel, E. H. (1945). "Emotional behavior of grey Norway and Wistar albino rats." *J. comp. Psychol.*, **38**, 109-18.
14. Finger, F. W. (1943). "Factors influencing audiogenic seizures in the rat. II. Heredity and age." *J. comp. Psychol.*, **35**, 227-32.
15. Griffiths, W. J. (1942). "Transmission of convulsions in the white rat." *J. comp. Psychol.*, **34**, 263-77.
16. Griffiths, W. J. (1944). "Absence of audiogenic seizures in wild Norway and Alexandrine rats." *Science*, **99**, 62-3.
17. Haldane, J. B. S. (1946). "The interaction of nature and nurture." *Ann. Eugen. Camb.*, **13**, 197-205.
18. Hall, C. S. (1938). "The inheritance of emotionality." *Sigma Xi Quart.*, **26**, 17-27, 37.
19. Hall, C. S. (1941). "Temperament: A survey of animal studies." *Psychol. Bull.*, **38**, 909-43.

20. Hall, C. S. (1947). "Genetic differences in fatal audiogenic seizures between two inbred strains of house mice." *J. Hered.*, **38**, 3-6.
 21. Hall, C. S. (1951). "The genetics of behavior." In Stevens, S.S. (Ed.) *Handbook of experimental psychology*. New York: Wiley & Sons.
 22. Hebb, D. O. (1949). *The organization of behavior*. New York: Wiley & Sons.
 23. Hollander, W. F. (1938). "'Clumsy' pigeons." *J. Hered.*, **29**, 65-6.
 24. Huestis, R. R., and Barto, E. (1936). "An inherited tremor in *Peromyscus*." *J. Hered.*, **27**, 436-8.
 25. Keeler, C. E. (1948). "Materials for the synthesis of hereditary behavior trends in mammals." *J. comp. physiol. Psychol.*, **41**, 75-81.
 26. Maier, N. R. F. (1943). "Studies of abnormal behavior in the rat: XIV. Strain differences in the inheritance of susceptibility to convulsions." *J. comp. Psychol.*, **35**, 327-35.
 27. Maier, N. R. F., and Glaser, N. M. (1940). "Studies of abnormal behavior in the rat: V. The inheritance of the 'neurotic pattern.'" *J. comp. Psychol.*, **30**, 413-18.
 28. Martin, R. F., and Hall, C. S. (1941). "Emotional behavior in the rat. V. The incidence of behavior derangements resulting from air-blast stimulation in emotional and non-emotional strains of rats." *J. comp. Psychol.*, **32**, 191-204.
 29. Patton, R. A. (1947). "Purulent otitis media in albino rats susceptible to sound-induced seizures." *J. Psychol.*, **24**, 313-17.
 30. Penrose, L. S. (1949). *The biology of mental defect*. London: Sedgwick & Jackson.
 31. Phillips, J. C. (1912). "Note on wildness in ducklings." *J. Anim. Behav.*, **2**, 363-4.
 32. Rasmussen, E. W. (1939). "Wildness in rats." *Acta Psychol. (Hague)*, **4**, 295-304.
 33. Rundquist, E. E. (1933). "Inheritance of spontaneous activity in rats." *J. comp. Psychol.*, **16**, 415-38.
 34. Russell, W. L. (1941). "Inbred and hybrid animals and their value in research." In: Snell, G. D. (Ed.) *Biology of the laboratory mouse*. Philadelphia: Blakiston.
 35. Scott, J. P. (1942). "Genetic differences in the social behavior of inbred strains of mice." *J. Hered.*, **33**, 11-15.
 36. Searle, L. V. (1949). "The organization of hereditary maze-brightness and maze-dullness." *Genet. Psychol. Monogr.*, **39**, 279-325.
 37. Stone, C. P. (1932). "Wildness and savageness in rats of different strains." In Lashley, K. S. (Ed.) *Studies in the dynamics of behavior*. Chicago: Univ. of Chicago Press.
 38. Tryon, R. C. (1931). "Studies in individual differences in maze ability. V. Luminosity and visual acuity as systematic causes of individual differences and an hypothesis of maze ability." *J. comp. Psychol.*, **12**, 401-20.
 39. Tryon, R. C. (1940). "Genetic differences in maze-learning ability in rats." *Yearbook Nat. Soc. Study Educa.*, **39** (1), 111-19.
 40. Tryon, R. C. (1942). "Individual differences." In Moss, F. A. (Ed.) *Comparative psychology*. New York: Prentice-Hall.
 41. Whitney, L. F. (1929). "Heredity of the trail-barking propensity in dogs." *J. Hered.*, **20**, 561-2.
 42. Whitney, L. F. (1932). "Inheritance of mental aptitudes in dogs." *Proc. 6th int. Congr. Genet. [Ithaca, N.Y.]*, **2**, 211-12.
 43. Witt, G. M., and Hall, C. S. (1949). "The genetics of audiogenic seizures in the house mouse." *J. comp. physiol. Psychol.*, **42**, 58-63.
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